Restoring *Aristida*stricta to *Pinus*palustris Ecosystems on the Atlantic Coastal Plain, U.S.A.

Kenneth W. Outcalt¹ Marcus E. Williams² Oghenekome Onokpise²

Abstract

Aristida stricta (wiregrass), a perennial bunchgrass, quickly accumulates dead leaves, which along with the shed needles of Pinus palustris (longleaf pine) provide the fuel for frequent surface fires. Thus, historically, wiregrass played a key role in many longleaf communities where it significantly influenced the natural fire regime and thereby the composition of the plant community. Reestablishment of wiregrass is, therefore, critical to restoring the native understory of Atlantic Coastal Plain longleaf pine ecosystems. This study measured the effects of different site preparations and fertilizer application on the survival and growth of wiregrass seedlings. Two-month-old seedlings were underplanted in existing longleaf pine stands on dry Lakeland soils at the Savannah River Site in South Carolina. Survival was acceptable at 51% after four years, although reduced owing to drought and small seedling size. Survival and growth could both be increased by using older seedlings with an initial height of at least 6 cm. Wiregrass leaves grew quite rapidly and attained an average length of 48 cm in four years on control plots. Basal area growth rate was greater than expected, averaging 40% on control treatments and 55% on cultivated and fertilized plots.

¹USDA Forest Service, Southern Research Station, Athens, GA 30602, U.S.A.

If growth rates during the first four seasons continue, wiregrass will attain mature size on cultivated and fertilized plots at six years, while non-fertilized control plots will take eight years. A planting density of one seedling per m² is recommended to provide sufficient wiregrass foliar cover to influence fire regimes in a reasonable length of time (i.e., 5–7 years).

Introduction

A ristida stricta (wiregrass) was once a major understory species in natural stands dominated by Pinus palustris (longleaf pine) on the Atlantic Coastal Plain (Abrahamson & Hartnett 1990; Myers 1990; Stout & Marion 1993). These pine wiregrass communities covered approximately 10 million ha from North Carolina to Florida (Southern Section, Society of Range Management 1974). Prior to fragmentation of the landscape, fire was a frequent natural occurrence (every 2–8 years) across much of the wiregrass range (Christensen 1981; Abrahamson & Hartnett 1990; Ware et al. 1993).

Wiregrass, a perennial bunchgrass, has an average natural density of five bunches per square meter (Clewell 1989). Leaves typically arch outward from the center of the bunch and overlap with adjoining individuals. The leaves are short-lived; 85% die within 12 months of formation (Parrott 1967). Once dead, leaves remain attached to the plant (Landers 1991) and decay quite slowly (Christensen 1993). Living and dead wiregrass leaves intercept needles shed by the overstory pines. This results in the accumulation of dead biomass in a very flammable configuration, which reaches a peak of 6160 to 7840 kg/ha in three to four years (Parrott 1967). Lightning-caused fires can spread quickly through this highly flammable fine-fuel matrix (Abrahamson & Hartnett 1990). Thus, wiregrass is critical for carrying frequent and evenly burning surface fires. These fires regulate plant composition and favor those species that survive frequent fires. The longleaf pinewiregrass ecosystem is maintained by these fires which inhibit the establishment and growth of competitive but less fire-tolerant species (Clewell 1989).

Over the last 200 years human activities have adversely affected the longleaf pine-wiregrass community. The combination of agricultural and forestry operations and decades of fire suppression have reduced the area occupied by longleaf pine to less than 1.2 million ha (Outcalt & Sheffield 1996). The area containing a generally intact understory is considerably less than that (0.5–0.8 million ha) (Noss 1989). This understory is extremely important, not only as a carrier of fire, but also as a reservoir of biological diversity. The plant community is very diverse and has many endemic species that depend on it for continued existence (Hardin & White 1989). Sustaining this unique ecosystem requires

²College of Engineering Sciences, Technology and Agriculture, Florida Agricultural and Mechanical University, Tallahassee, FL 32307, U.S.A.

^{© 1999} Society for Ecological Restoration

management that will perpetuate the understory on areas where it still exists and restoration of the understory on critical sites where it has been eliminated or severely damaged. The reestablishment of wiregrass is a key part of restoring this important plant community.

Once eliminated from a site, wiregrass does not readily re-invade (Clewell 1989). Although it does reproduce vegetatively, the process is slow and results in only limited spread. For a number of years, it was widely assumed that wiregrass did not produce viable seeds (Myers 1990). More recent studies, however, have shown that wiregrass does produce viable seed in quantity following growing-season burns (Clewell 1989; Seamon et al. 1989; Outcalt 1994). Dissemination of seed into, and establishment of wiregrass seedlings on, previously unoccupied sites, however, appears to be a rare event. Therefore, reestablishment of wiregrass into areas where it has been extirpated requires the deliberate introduction of seeds or seedlings.

A fundamental question when establishing wiregrass seedlings is: what planting density and configuration are appropriate? This will depend on subsequent survival and growth rate of wiregrass seedlings. Clewell (1989) estimated that wiregrass clumps expand about 20% per year within well-established communities. Growth rates may be faster on sites with less competition, but documentation is lacking for this supposition. Also, very little information about increasing growth rates through cultural treatments is available. Restoration efforts to date have concentrated on sites without longleaf trees, where both wiregrass and longleaf have been reintroduced simultaneously (Stolzenburg 1991). Therefore, there is no information about how an existing overstory will affect wiregrass seedlings. The objective of this study was to determine wiregrass survival and its growth rates with different cultural treatments when underplanted in longleaf pine stands.

Methods

The study was located on the U.S. Department of Energy Savannah River Site in the west-central South Carolina region. This area has an average growing season of 285 days, an average winter temperature of 8.6°C (47.5°F) and an average summer temperature of 26.5°C (80°F). Annual precipitation averages 1200 mm, with about half falling between April and September. The Savannah River Site lies between the fall line area, where the Upper Coastal Plain meets the Piedmont, and the Savannah River. It contains about 15,000 ha of droughty sandhills land suitable for the longleaf community. Although the historical abundance of wiregrass in the area is not known, it clearly did, and still does, occur there. While this does not mean that wiregrass was the dominant grass on all longleaf sites, past

agricultural use and a long-term absence of fire very likely reduced its abundance significantly.

For the study, three sites were randomly selected from all the longleaf pine stands on the Savannah River Site with trees greater than 40 years old. All selected longleaf stands were old field sites where longleaf was established by direct seeding in the mid 1950s. Average stocking, for trees with diameters greater than 3 cm, was 226 longleaf pine per ha and 25 oaks per ha, comprised of Quercus laevis (turkey), Q. incana (bluejack), and Q. hemisphaerica (laurel). The average diameter was 29.5 cm for longleaf pine and 12 cm for the oaks. Longleaf pine had a basal area of 10 m² per ha. Soil on all blocks was Lakeland sand (thermic, coated Typic Quartzipsamment) which is predominantly sand with 5-10% silt plus clay and 1% organic matter. Most midstory oaks had been removed by hand felling in 1991, followed by prescribed burning in the spring of 1992 that eliminated most oak sprouts. Because the tree densities in these stands were high until thinning was begun at age 30, the understory was very sparse. Pineneedle litter was the most common ground cover on sites one and two, averaging about 70%. The most common understory species were Vaccinium stamineum with lesser amounts of V. elliotti and V. arboreum (blueberries) collectively contributing 10% cover, and Andropogon gerardi and A. virginicus (broomsedge) with 5% cover. The third site had an understory dominated by blueberries (50%) and pine needles (40%).

A randomized block split-plot design with three blocks, two main plots in each block, and three treatment sub-plots per main plot was used. An 80×120 -m block was established in each of the three selected longleaf stands. Each block was then divided into two 40×120 -m main plots, with one assigned to receive a fertilizer treatment. The main plots were further sectioned into three 40×40 -m sub-plots to measure the effects of different methods of site preparation. Each subplot had a 20×20 -m central treatment area and 10-m buffer strips. Site preparation treatments consisted of mechanical cultivation, herbicide application, or a notreatment control randomly assigned to one sub-plot in each main plot. In early April 1993 a garden tiller was used to cultivate 1-m-wide strips spaced 2 m on center to a depth of 20 cm. Herbicide sub-plots received a 3 ml dose of 25% active ingredient hexazinone liquid applied with a backpack sprayer and a calibrated spot gun one week after wiregrass seedlings had been planted. Hexazinone was sprayed in spots spaced 2 m apart between rows of wiregrass plants at an application rate of 2.2 kg active ingredient per ha. When applied in this spot-grid pattern, hexazinone selectively targets woody species (Brockway et al. 1998).

The wiregrass seed came from the Carolina Sandhills National Wildlife Refuge, which is located 160 km to

the northeast of the study site near McBee, South Carolina. During December, 1992 National Forest System personnel hand collected wiregrass seeds across a 40-ha site burned the previous May. A contractor grew the seedlings in a greenhouse near Aiken, South Carolina. Between 10 and 20 wiregrass seeds with a mean viability of 15% were sown in a standard potting mixture of peat and vermiculite. The square, tapered plastic containers used were 57×57 mm on top, 35×35 mm on the bottom, and 75 mm high. Seedlings were kept in the greenhouse for about two months following completion of germination around 1 March. In late April 1993, 100 wiregrass plugs were hand planted in each treatment sub-plot at 2×2 -m spacing arranged as 10 rows with 10 seedlings each. All plugs were watered following planting. Seedlings began with an average of eight leaves per plug and were 4 cm tall one week after planting. Wiregrass plants on one main plot in each of the three blocks were fertilized at the beginning of the second growing season (May 1994). A 30 × 30-cm area around each wiregrass plant was fertilized at a rate of 175 kg per ha with a 16-4-8 mixture containing 3.8% slow-release nitrogen. During the first week of June 1995, plots that had been treated with hexazinone were prescribed burned using strip headfires.

One week after planting, the number of leaves and length of longest leaves were determined for each wiregrass plug. The wiregrass seedlings were measured again at one month and then at the end of each growing season thereafter. Basal diameters were measured at two points perpendicular to each other at the ground line of each grass clump with a caliper. Average diameter was used to calculate basal area. The dimensions of wiregrass leaf-spread were used to calculate area covered. Data for each year were analyzed separately with analyses of covariance using initial measurements as the covariant. NCSS, a statistical software package, was used for the analyses (Hintze 1995). Significant differences between predetermined means were calculated using Fisher's least significant difference measure, when the covariant analyses yielded a significant F statistic. At the end of the fourth growing season, the dom-

Table 1. Survival (%) of underplanted wiregrass by site preparation treatment at Savannah River Site, South Carolina.

Treatment	Growing Season					
	1 Month	First	Second	Third	Fourth	
Control Hexazinone Cultivation	63ª* 54ª 64ª	59 ^b 44 ^a 62 ^b	57 ^b 43 ^a 61 ^b	56 ^b 39 ^a 60 ^b	56 ^b 38 ^a 60 ^b	

^{*}Letters denote significant differences between means in the same column at the 0.05 level (power = 0.69 at α = 0.05) based on a significant F and Fisher's least significant difference.

inant ground cover around each planting spot was recorded. The effect of competing vegetation on wiregrass survival was assessed using ground cover data in contingency tables and the chi-square statistic.

Result

Survival

Mortality of newly planted wiregrass plugs occurred very quickly with a 40% loss after one month (Table 1). Wiregrass seedlings had very little additional mortality, however, during the remainder of the first growing season, except on plots treated with hexazinone. This additional mortality resulted in significantly lower survival than under the other treatment regimes. Cultivation did not significantly improve first-year survival compared to untreated control plots. A few wiregrass plants died during the second growing season but survival was relatively constant on control and cultivated plots through four growing seasons. Survival declined slightly following prescribed burning in June 1995. Although it was highest on cultivated plots after four growing seasons, survival did not differ significantly from the control (power = 0.69 at α = 0.05). Competition from blueberries decreased wiregrass survival while survival was higher on spots dominated by pine straw (Table 2). These differences were significant for each site preparation treatment tested separately and for all treatments combined.

Leaf Growth

On the non-fertilized control plots, wiregrass plants had a linear increase in maximum leaf length during the first three growing seasons (Fig. 1), then slowed slightly between the third and fourth growing season, peaking at around 50 cm. A very significant covariant in all data analyses showed that initial leaf length affected subsequent growth of wiregrass plugs. Maximum leaf length of wiregrass at the end of each growing season was positively related to leaf length at

Table 2. Dominant vegetation around wiregrass planting spots after fourth growing season as percent of total spots in that class.

Dominant Vegetation	All Planting Spots	Planting Spots with Live Wiregrass	
Grass	7a*	7ª	
Oaks [®]	3^a	3^a	
Blueberries	26^{b}	154	
Pine Straw	64^a	75 ^b	

^{*}Letters denote significant differences between means in the same column at the 0.05 level as determined by contingency tables and chi-square tests.

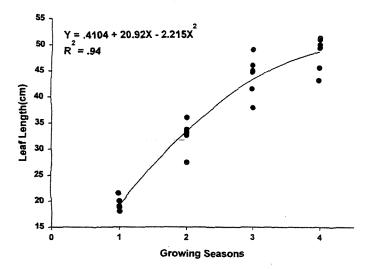


Figure 1. Growth curve for leaves of wiregrass, underplanted without site preparation in longleaf pine stands at Savannah River Site, South Carolina.

outplanting. This is illustrated by the increasing trend in leaf length at the end of the fourth growing season for seedlings with longer leaves at planting (Fig. 2). The combination of cultivation and fertilizer increased final leaf length of all seedlings, but the general relationship of seedlings with longer leaves at planting yielding longer leaves after four seasons was still true.

Neither hexazinone application nor cultivation affected maximum leaf length during the first growing season (Fig. 3). Fertilizer application at the beginning of the second growing season significantly increased leaf growth across all treatments. There was a strong interaction between treatment and fertilizer with the greatest gains in total leaf length occurring on cultivated plots that were fertilized. Prescribed burning of the

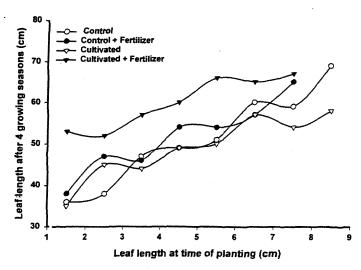


Figure 2. Relationship of initial wiregrass leaf length to maximum leaf length after four growing seasons.

hexazinone plots at the beginning of the third growing season reduced maximum leaf length that year. The fertilizer effect continued into the third growing season when leaf length was significantly higher, especially where fertilization had been combined with cultivation. During the fourth growing season, maximum leaf length remained static on the previously fertilized control and cultivated plots, while it continued to increase on other plots.

Basal Area Growth

Site preparation treatments had no effect on wiregrass basal area growth the first season (Fig. 4). Fertilization at the beginning of the second growing season significantly increased basal area growth on all treatments. This was followed, however, by a year of lower growth on fertilized plots and better wiregrass basal area growth on the non-fertilized plots. There appears to have been a slight loss in basal area owing to the prescribed burning of hexazinone plots, but it was not significant. Wiregrass plants had equal basal area growth on all treatment and fertilizer combinations over the fourth growing season, except where cultivation and fertilization had been combined. On these plots, mean wiregrass basal area doubled during the fourth growing season.

Foliar Cover

Fertilizer application in the second growing season increased wiregrass foliar cover (i.e., the area covered by

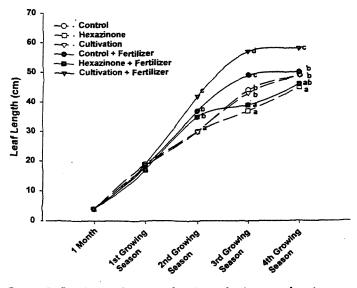


Figure 3. Leaf growth for underplanted wiregrass by site preparation treatment and fertilizer level at Savannah River Site, South Carolina. Letters denote significant differences between treatment means at the end of a growing season based on a significant F and Fisher's least significant difference.

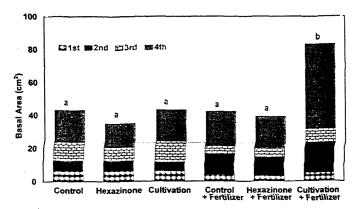


Figure 4. Basal area growth over four growing seasons, by treatment for underplanted wiregrass in longleaf pine stands at the Savannah River Site, South Carolina. Letters above treatments denote significant differences in basal area after four growing seasons at 0.05-level based on significant F and Fisher's least significant difference.

the spreading leaves of the plant; Table 3). As before, plants on cultivated plots benefited the most—nearly doubling in size—compared to unfertilized plants. Prescribed burning at the beginning of the third season significantly reduced wiregrass foliar cover on the hexazinone plots. The fertilizer effect was still evident the third growing season on the cultivated treatments, where plants remained nearly twice as large as on other plots. Foliar cover values changed little over the fourth growing season except on previously burned hexazinone plots, which regained cover that had been lost to fire.

Discussion

Survival

Wiregrass seedling mortality during the month following planting was rather high on all plots. Uridel (1994) also reported the greatest mortality occurred during the first three weeks following outplanting. Lack of soil

Table 3. Wiregrass foliar cover (cm²) by time and treatment when underplanted in existing longleaf pine stands at Savannah River Site, South Carolina.

	Growing Season			
Treatment	Second	Third	Fourth	
Control	860a*	3540°	3850ª	
Hexazinone	840ª	2260a	3540a	
Cultivation	800ª	2870 ^b	3600ª	
Control + Fertilizer	1130 ^b	3655°	3890ª	
Hexazinone + Fertilizer	975 ^b	2185^{a}	3410a	
Cultivation + Fertilizer	1650°	6450 ^d	5770b	

^{*}Letters denote significant differences between means in the same column at the 0.05 level (power = 0.999 at α = 0.05) based on a significant F and Fisher's least significant difference.

moisture likely caused much of the early mortality in our study. South Carolina experienced a 100-year drought in 1993 with only trace amounts of rainfall received in April at the Savannah River Site. For the entire growing season, rainfall across the site averaged only 225 mm, about half the normal amount. Also, mortality was especially high—averaging nearly 70%—across block three. The block was the highest in elevation and the most xeric of the sites, with only a very sparse litter layer to conserve soil moisture. Kindell (1994) also indicated wiregrass seedling survival was dependent on rainfall and soil moisture. Another factor contributing to mortality was the size and age of the wiregrass plugs. The plugs were only 2-3 months old when outplanted and many were rather small. Mortality rate for the smallest wiregrass plants (i.e., those plugs with fewer than five leaf blades at the time of planting) was over 70% whereas larger plugs had mortality rates under 15%.

The lower survival on plots treated with hexazinone may have resulted from the treatment, but this seems unlikely. The hexazinone was applied in spots between wiregrass plugs one week after seedlings were planted. With the low rainfall, it is highly unlikely that enough herbicide to cause mortality could have reached wiregrass plants. The lower survival was largely caused by very high mortality on one plot in block three. That plot had very little longleaf overstory, and blueberries, which had an average cover for the entire block of 50% dominated 89% of the planting spots. The lack of overstory shade and interspecific competition for soil moisture likely contributed to the poor survival. In addition, the plot was planted last and received a large number of very small wiregrass plants. The combination of these factors resulted in a mortality rate of 94%.

The fact that many wiregrass seedlings were able to survive outplanting during a 100-year drought attests to the tenacity of this species. Survival was over 60% on all areas except for block three, the driest site where blueberry cover was high. Thus, wiregrass can be successfully established by planting containerized plugs under a moderate-to-low density overstory. Seamon et al. (1989) recommend using seedlings 1–2 years old when planting open areas. This may not be necessary when underplanting wiregrass, but in view of the relationship between size and survival, planting seedlings that are six rather than two months old seems appropriate. Because seedlings grown in larger containers seem to survive better on harsh sites (Duever 1989), larger plugs should also be considered for very dry sandy areas.

Leaf Growth

The relationship between initial leaf length and final seedling size resulted from the lower average growth rates for those smaller-than-average wiregrass plugs that did survive. Thus, culling small wiregrass plants before planting would likely improve growth rates. If a maximum leaf length of 50 cm after four growing seasons is desired, then seedlings below 6 cm at planting time should not be used. It appears that cultivation and fertilizer combined stimulated growth enough so that even very small seedlings with leaves 1.5 cm long reached 50 cm in length after four seasons. However, this treatment did not improve survival of small seedlings and, therefore, it would still be beneficial to cull small seedlings before planting.

Even though precipitation was far below normal, average leaf growth of the wiregrass was fair. Plants with leaves 4 cm long at one month had leaves 18 cm long at the end of the first growing season. This is only about half the total height reported by Uridel (1994) for wiregrass after one season when planted in plowed strips. However, the wiregrass plants used in his study were much larger transplants that had been gathered from natural populations. The larger 2-year-old seedlings within prescribed-burn areas followed more closely the growth pattern of the transplants used by Uridel (1994), which had been clipped prior to planting. Fire in our study set leaf length back to nearly zero, but the wiregrass recovered quickly and in a single season had grown back to pre-burn average length. The following season, leaf growth resumed, following a pattern similar to unburned plants.

Where containerized wiregrass seedlings produced from seed are outplanted and no fertilizer is added, maximum leaf length can be expected to increase linearly for the first three years. It will slow slightly between the third and fourth growing season, peaking at around 50 cm on dry sandy sites. Fertilization after establishment speeds up the growth rate, causing wiregrass to reach maximum leaf length a year sooner. However, such fertilization does not significantly increase maximum length.

Site Preparation

Herbicide application has been shown to increase survival and growth of wiregrass planted in *Paspalum notatumn* (bahia grass) pastures (Uridel 1994). In our study, however, wiregrass underplanted into longleaf pine stands did not benefit from hexazinone application. Much of the woody competition had been removed prior to study installation by hand felling and prescribed burning. What woody competition remained consisted mostly of blueberries, which are very tolerant of hexazinone (Wilkins et al. 1993). To be effective, hexazinone must be transported into the plant via water uptake. Because there was not enough precipitation during the dry spring and early summer to transport it

into the plants, hexazinone was largely ineffective in controlling the remaining woody species. Thus, the lack of response to hexazinone is attributed to low susceptibility of blueberries and a lack of precipitation.

Uridel (1994) found cultivation effective in reducing competition from bahia grass and increasing growth of planted wiregrass. The lack of a significant response to cultivation on our sites was likely the result of a low density of herbaceous vegetation. Although grasses and forbs were present on all study sites, there was not a continuous, established layer as is found in old pastures. Because the 40-year-old stands used for the study had a fairly dense over story for the first 30 years following establishment, herbaceous cover only dominated 7% of the planting spots after four growing seasons, whereas pine needle litter dominated 64%. However, cultivation was very beneficial when combined with fertilization. Although fertilization increased leaf length, basal area, and foliar cover of wiregrass on control plots, the effect lasted only one year. When combined with cultivation, however, the fertilizer effect continued into later growing seasons. Combining these treatments resulted in a doubling of basal area, three growing seasons after fertilization. This was probably the result of fewer tree roots in cultivated strips, which allowed wiregrass plants to capture additional nutrients. Caution should be used on sites with more well-developed ground cover, because fertilization may also stimulate competing vegetation, thereby reducing survival and growth of wiregrass plants.

Prescribed Burning

Because hexazinone was not effective in reducing competition and did not influence growth compared to the control, it provided us with the opportunity to explore the effect of prescribed burning on young wiregrass seedlings. This is based on the assumption that all effects following prescribed burning were due to the fire and not some carryover from the hexazinone treatments. It is well established that growing-season fires stimulate flowering and seed production by mature, established wiregrass plants (Clewell 1989; Seamon et al. 1989; Outcalt 1994). A few plants in this study produced flowers during the second growing season. During the third growing season, 16% of the wiregrass on plots that were burned that June produced seed, but less than 1% of plants on unburned plots flowered. Thus, even relatively small wiregrass seedlings will respond to burning with increased seed production. Most plants, however, had fewer than five seed stalks and less than 20 seeds per stalk. Although 17% of the seeds tested as viable, the probability of significantly increasing the population from these few seeds would be small. After four growing seasons, the seed produced has not resulted in any new wiregrass seedlings on any of the plots.

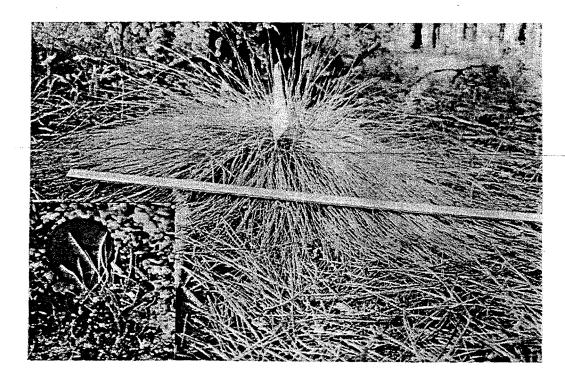


Figure 5. wiregrass seedling one week after planting (inset with camera lens cover) and after four growing seasons (with meter stick) on cultivated and fertilized treatment.

Moore et al. (1982) reported that fire can also stimulate vegetative growth of mature wiregrass plants and increase total aboveground biomass. In our study, prescribed burning at the onset of the third growing season killed some of the smaller wiregrass plants and caused a reduction in maximum leaf length among the survivors. Thus, until wiregrass is well established in four or five years, prescribed burning is unnecessary unless re-

quired for control of woody plant competition. In such cases, wiregrass plants as young as two years old will likely survive the burn.

Basal Area Growth

Mature wiregrass plants are reported to have mean basal diameters of 23 cm and a basal area of 415 cm² on



Figure 6. wiregrass bunches four growing seasons after planting under longleaf pine on a cultivated and fertilized area at the Savannah River Site, South Carolina.

dry sandy sites (Outcalt 1994). After four growing seasons, wiregrass on non-fertilized control plots averaged 7.4 cm in diameter and had a basal area of 43 cm², whereas on cultivated and fertilized plots, the average diameter was 10 cm and the basal area 83 cm². Thus, wiregrass plants had attained a basal area equal to 10 and 20% of expected mature size on control and cultivated plus fertilized plots, respectively, in just four growing seasons. Clewell (1989) estimated wiregrass had a basal diameter growth rate of 20% per year, and that it would take 15 years to reach mature size. Wiregrass basal diameter growth on the control plots averaged 40% per year, whereas on cultivated plus fertilized plots it averaged 55%. If this growth rate continues, wiregrass on cultivated and fertilized plots will reach mature size in six years. Even on non-fertilized control plots it will take only eight years to reach mature size. Thus, when wiregrass is underplanted into areas without a lot of competition, its growth rates can be much higher than previously reported for wiregrass growing on sites with a well-established and competitive understory layer.

Foliar Cover

The real measure of success in reestablishing wiregrass is foliar cover. One of the critical roles of wiregrass in the ecosystem is its influence on fire. This requires enough wiregrass cover to provide fuel, to intercept falling pine needles, and to promote fire spread between wiregrass bunches. After four growing seasons, the mean foliar cover on non-fertilized control plots was about 3850 cm², or nearly 10% of the surface area of the 4-m² planting site. On the cultivated plus fertilized plots where plants were largest (Fig. 5), wiregrass still only covered 14% of the area (Fig. 6). If, however, planting had been done on 1-m centers, wiregrass would have covered 20% of the control and 35% of cultivated plus fertilized plots. In addition, with 1 m between plants and a leaf length of 0.5 m, the leaves of adjoining plants would be touching. On the cultivated plus fertilized plots, the level of cover and continuity of wiregrass leaves would be sufficient to promote evenly burning surface fires. Thus, planting wiregrass plugs on cultivated strips at 1×1 -m spacing, combined with fertilization during the second growing season, should provide enough cover after 4-5 years to sustain desirable fire characteristics. Although it may take 2-3 years longer to reach comparable cover levels on unfertilized plots, this would still be a reasonable time span for reestablishing wiregrass as a significant understory component of longleaf pine communities. The possible adverse effects and costs of fertilizer additions make these treatments a better choice for many sites. The additional fuels provided by naturally disseminated grasses and

forbs can also reduce the time needed to achieve desirable burning conditions.

Acknowledgments

We are grateful to D. Brockway, J. Putz, A. Clewell, and an anonymous reviewer for comments that improved this manuscript. Funding for and assistance in conducting this study were provided by the Department of Energy through USDA Forest Service, Savannah River Natural Resource Management and Research Institute, Biodiversity Research Program, Aiken, South Carolina, U.S.A.

LITERATURE CITED

- Abrahamson, W. G., and D. C. Hartnett. 1990. Pine flatwoods and dry prairies. Pages 103–149 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando.
- Brockway, D. G., K. W. Outcalt, and R. N. Wilkins. 1998. Restoring longleaf pine wiregrass ecosystems: plant cover, diversity, and biomass following low-rate hexazinone application on Florida sandhills. Forest Ecology and Management 103: 159–175
- Christensen, N. L. 1981. Fire regimes in southeastern ecosystems. Pages 112–135 in Fire regimes and ecosystem properties. U.S. Department of Agriculture, Forest Service General Technical Report WO–26. Forest Service, Washington, D. C.
- Christensen, N. L. 1993. The effects of fire on nutrient cycles in longleaf pine ecosystems. Pages 205–214 in S. H. Hermann, editor. Proceedings of the 18th Tall Timbers Fire Ecology Conference: The longleaf pine ecosystem: ecology, restoration and management, 30 May-2 June 1991, Tallahassee. Tall Timbers Research Station, Tallahassee, Florida.
- Clewell, A. F. 1989. Natural history of wiregrass (Aristida stricta Michx., Gramineae). Natural Areas Journal 9:223-233.
- Duever, L. C. 1989. Research priorities for the preservation, management, and restoration of wiregrass ecosystems. Natural Areas Journal 9:214–218.
- Hardin, E. D., and D. L. White. 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Natural Areas Journal 9:234–245.
- Hintze, J. L. 1995. User's guide NCSS 6.0 statistical system for windows. Number Cruncher Statistical Systems, Kaysville, Utab.
- Kindell, C. 1994. Adaptive population differentiation in wiregrass (Aristida stricta) in north Florida sandhills and flatwoods. Page 25 in A. F. Clewell and W. Cleckley, editors. Proceedings of the Wiregrass Ecosystem Restoration Workshop, 22 April 1994, Tallahassee. Northwest Florida Water Management District, Tallahassee.
- Landers, J. L. 1991. Disturbance influences on pine traits in the southeastern United States. Pages 61–98 in Proceedings of the 17th Tall Timbers Fire Ecology Conference; High Intensity Fire in Wildlands, 18–21 May 1989, Tallahassee. Tall Timbers Research Station, Tallahassee, Florida.
- Moore, W. H., B. F. Swindel, and W. S. Terry. 1982. Vegetative response to prescribed fire in a north Florida flatwoods forest. Journal of Range Management 35(3):386–389.
- Myers, R. L. 1990. Scrub and high pine. Pages 150–193 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando.

- Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Natural Areas Journal 9: 211–213.
- Outcalt, K. W. 1994. Seed production of wiregrass in central Florida following growing season prescribed burns. International Journal of Wildland Fire 4:123–125.
- Outcalt, K. W., and R. M. Sheffield. 1996. The longleaf pine forest: trends and current conditions. U.S. Department of Agriculture, Forest Service Resource Bulletin SRS-9. Southern Research Station, Asheville, North Carolina.
- Parrott, R. T. 1967. A study of wiregrass (*Aristida stricta* Michx.) with particular reference to fire. M. S. thesis. Duke University, Durham, North Carolina.
- Seamon, P. A., R. L. Myers, L. E. Robbins, and G. S. Seamon. 1989. Wiregrass reproduction and community restoration. Natural Areas Journal 9:264–265.
- Southern Section, Society of Range Management. 1974. Range resources of the South. Georgia Agriculture Experiment Station, College of Agriculture Bulletin N.S. 9. University of Georgia, Athens.

- Stolzenburg, W. 1991. The wiregrass mystery. Nature Conservancy, 41(5):28–29.
- Stout, I. J., and W. R. Marion. 1993. Pine flatwoods and xeric pine forest of the Southern (lower) Coastal Plain. Pages 373–446 in W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the southeastern United States, lowland terrestrial communities. John Wiley & Sons, New York.
- Uridel, K. W. 1994. Restoration of native herbs in abandoned *Paspalum notatum* (Bahia grass) pastures. M.S. thesis. University of Florida, Gainesville.
- Ware, S., C. Frost, and P. D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pages 447-493 in W. H. Martin, S. G. Boyce, and A. C. Echternacht, editors. Biodiversity of the southeastern United States, lowland terrestrial communities. John Wiley & Sons, New York.
- Wilkins, R. N., W. R. Marion, D. G. Neary, and G. W. Tanner. 1993. Vascular plant community dynamics following hexazinone site preparation in the lower Coastal Plain. Canadian *Journal of Forest Research* 23:2216–2229.